Aquatic Mammals 2019, *45*(2), 233-243, DOI 10.1578/AM.45.2.2019.233

Diel Dive Behavior of Fin Whales (*Balaenoptera physalus*) in the Southern California Bight

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Abstract

While many baleen whale species exhibit temporal patterns in their diving behavior, our understanding of these patterns have often been drawn from short duration tags and a small number of individuals. Herein, we describe extended patterns of diving behavior and vertical habitat use of 10 fin whales in the Southern California Bight (SCB) that were tagged with dive-and-location reporting satellite transmitters (total data collection 245.4 d; mean data per whale 24.5 d). Dive behavior was strongly diel and consisted of two primary modes: (1) prolonged use of the upper water column (< 20 m) at night and (2) daytime dives of variable depth. The crepuscular periods exhibited gradual transition between these modes: at dawn, dives became progressively deeper; and at dusk, they were progressively shallower. Although the median percentage of time spent at or immediately below the surface (< 5 m) was roughly equal between day and night, the percentage spent above 20 m depth increased from 42% during the day to 58% at night ($p < 0.001$), and whales spent virtually all nighttime hours above 40 m. Diving behavior also appeared to vary seasonally. These whales spent the greatest proportion of time in the upper water column during spring and winter nights. Data from two tagged animals that left the SCB suggest these patterns may extend beyond the region. These findings suggest that exposure to surface-oriented risk—in particular, vessel collision—also varies temporally and underscore the importance of developing mitigation measures that are robust to nighttime conditions. Fin whales are the most frequently ship-struck species in the region, and their tendency to use surface waters most when they are least detectable may be a contributing factor.

Key Words: diel dive behavior, fin whale, *Balaenoptera physalus*, Argos, Southern California Bight, dive strategy, ship strike

Introduction

Many previous studies have suggested Balaenopterid whales exhibit strong diel modes in feeding behavior, conducting progressively shallower dives at dusk, presumably in response to vertically migrating prey. These studies include observations of two fin whales (*Balaenoptera physalus*) in the Mediterranean Sea (Panigada et al., 1999, 2003) and one off southern California (Friedlaender et al., 2015); a blue whale (*Balaenoptera musculus*) in the Sea of Cortez (Calambokidis et al., 2007) and one off southern California (Friedlaender et al., 2015); and humpback whales (*Megaptera novaeangliae*) in the Antarctic (Friedlaender et al., 2013, 2016; Tyson et al., 2016), Stellwagen Bank (Friendlaender et al., 2009), and Alaska (Burrows et al., 2016). Long nighttime surface periods were also observed in fin and blue whales off southern California (Friedlaender et al., 2015), and diel modes in vocal activity have been observed in several species (e.g., blue whales in the Southern California Bight [McKenna et al., 2009] and fin whales in the northeast Pacific [Širović et al., 2013]). Diel dive behaviors have also been observed in other cetacean families, including Physeteridae (Aoki et al., 2007) and Delphinidae (Baird et al., 2001, 2002). However, most of the previous studies relied on short-term (typically hours long) tag deployments, and published observations for fin whales are limited to a small number of individuals with limited seasonal coverage. Therefore, it is not known if or how these diel behavioral patterns might persist across a larger sample of whales or within the same individual over time. It is particularly important to identify any predictable patterns in vertical habitat use along the U.S. West Coast where fin whales are the most frequently ship-struck large whale (NOAA unpub. data, 2009-2015) as they might help inform more appropriate mitigation strategies.

Herein, we describe the vertical habitat use of 10 fin whales tagged off the coast of southern California for periods ranging from 6 to 83 d. We characterize diel and seasonal differences in the use of the immediate surface zone and the upper water column, and we discuss the implications of those differences in terms of interactions with anthropogenic threats, with particular attention to ship strikes.

Methods

Data Collection

Tag Deployments—SPLASH10-292 Argos-linked dive recorders in the LIMPET configuration (Wildlife Computers, Redmond, WA, USA; Andrews et al., 2008; Schorr et al., 2014) were deployed on fin whales in the Southern California Bight (SCB) using a Dan-Inject J.M.SP.25 pneumatic projector (Børkop, Denmark). Tags were deployed at ranges between 5 and 20 m from a rigid-hull inflatable research vessel and attached on or near the dorsal fin. Reactions were categorized following Berrow et al. (2002). Tags were deployed under NOAA/NMFS Permit #540-1811 and 16111 under protocols approved by the Cascadia Research Collective Institutional Animal Care and Use Committee.

Tag Programming—Dive data, measured with a pressure sensor with a 1 Hz sampling rate, were collected via the Behavior Log (BL), transmitted via Argos, and processed via the Wildlife Computers data portal (Wildlife Computers, 2017). Tags were user-programmed to record a qualifying dive in which the fin whale descended below 20 m for more than 30 s in the BL. Depth transitions were used to define the start and end times of dives, rather than the wet/dry sensor, because fin whales do not always bring their dorsal fin above the surface between dives, creating a potential for dive concatenation. Thus, the start and end time of each dive was marked when the whale passed a certain dive depth transition threshold (2 m for tags deployed before 2015, n = 8; 5 m for tags deployed after 2015, n = 2) on descent and ascent of qualifying dives. Time spans between qualifying dives, when the whale did not descend below 20 m for more than 30 s, were recorded as "surfacings." Each surfacing record included the total amount of time spent above and below the dive depth transition threshold. In general, five dives and five surfacings were packaged into a single BL message for transmission via Argos. If an Argos message failed to be received by a satellite or shore-based receiving station (Jeanniard-du-Dot et al., 2017), a gap in the BL occurred. For each qualifying dive, maximum depth was written to the BL in bins of up to ±1.5% of the actual maximum depth recorded during the dive. Pressure transducer depth readings for this same tag model and configuration were verified in a pressure chamber (Schorr et al., 2014). Each tag deployment was also assessed for pressure transducer function by reviewing the depth during Argos transmissions as recorded in status messages (Wildlife Computers, 2017) and a visual representation of the dive record.

Data Analysis

Argos location estimates for each tagged whale were filtered using the Douglas Argos filter (Douglas et al., 2012), using a maximum sustainable rate of movement of 20 km/h, retention of all location estimates class 2 and above, the default ratecoef (minimum accepted angle between three locations) of 25, and a maximum redundant distance setting of 3 km. The approximate location of each BL event (surfacing or dive) was interpolated along the track connecting sequential locations retained by the filter based on the event start time. Behavioral events were assigned to the standard meteorological seasons based on their date and time (winter = 22 December to 20 March; spring = 21 March to 21 June; summer = 21 June to 22 September). Solar elevation (the angle of the sun above or below the local horizon), lunar elevation, and lunar phase at the start of each behavioral event were assigned using the *R* package 'maptools' (Bivand & Lewin-Kah, 2017; R Core Team, 2018).

Data from each dive and the surfacing that followed it were combined into *dive cycles*. We estimated the percentage of each dive cycle spent within the upper water column (0 to 20 m) and two subsequent 10-m depth bins: 20 to 30 m and 30 to 40 m. For dives, the time within each bin was estimated using published ascent and descent speeds and angles (Table 1). Assuming an overall transit speed of 2.43 m s^{-1} and angle of 58.5°, we calculated the vertical transit rate (R_T; i.e., the vertical vector of transit speed) for our whales at 2.07 m s^{-1}. Time within a given depth bin (T_Z, with depth boundaries Z_{min} and Z_{max}) was calculated one of two ways depending on the maximum dive depth, using the assumption that animals transited directly to their maximum depth and stayed at that depth until transiting back to the surface. When dive depth was deeper than the lower boundary of a given depth window (Z_{max}), the following equation was used to determine time spent within (i.e., transiting through) the depth window:

$$T_Z = 2(Z_{max} - Z_{min})/R_T$$

When the dive depth fell between Z_{min} and Z_{max}, the following equation was used instead:

$$T_Z = T_D - (T_D - 2(Z_{min}/R_T))$$

Where T_D is the total dive duration. The second term in the subtraction is the round-trip transit time to Z_{min}. We also calculated the proportion of each surfacing that was spent at the surface itself (shallower than 2 or 5 m depending on tag

Table 1. Published means (standard deviations) of speeds and angles of dive descent and ascent that were used in our study to estimate proportion of dive cycle spent within depth windows

	Speeds (ms^{-1})		Angles (degrees)	
Study	Descent	Ascent	Descent	Ascent
Croll et al., 2001	2.00 (0.17)	1.70 (0.37)		
Goldbogen et al., 2006	3.70 (0.40)	2.40 (0.30)	53 (8)	64 (7)
Friedlaender et al., 2015	2.80 (0.30)	2.00 (0.20)		

programming) and between the dive depth transition threshold and 20 m as the depth a BL "dive" started recording. The following metrics were calculated for each dive cycle: maximum dive depth (m), difference in maximum depth between the current and subsequent cycle, dive duration (min), difference in dive duration between current and subsequent cycle, surface duration (min), mean solar elevation, mean lunar elevation, mean lunar phase, and the proportion of the cycle spent within the aforementioned depth bins.

Diel variation in dive metrics was evaluated using two methods. First, dive metrics were plotted as functions of solar elevation. A one-sample, two-sided Wilcoxon signed rank test, a nonparametric test appropriate for the non-normal distributions of our data, was used in the *R* package 'stats' (R Core Team, 2018) to superimpose a running pseudomedian (window size = 3° of solar elevation) atop the scatterplot along with 95% confidence intervals. The pseudomedian is a measure of centrality reported by the Wilcoxon test that is equivalent to the median in symmetrical distributions (Hollander & Wolfe, 1973). These plots made it clear that despite considerable data variation (Figure 1), most dive metrics had different night- and daytime distributions with a dynamic transition during crepuscular periods. This crepuscular transition zone occurred between solar elevations of approximately -20° and 0°.

Second, dive cycles were assigned to night- or daytime groups according to the transition zone defined above, with crepuscular data excluded. Statistical differences between night and day metrics were tested with a two-sample, two-sided Wilcoxon (Mann-Whitney U) test. Effect size was measured as the proportion of cases in which the pseudomedian of one diel mode exceeded the other (U/n_1n_2, where U is the test statistic, n_1 is the sample size of daytime dive cycles, and n_2 is the sample size of nighttime dive cycles). The same statistic was used to test for differences in dive behaviors between winter and summer seasons by assigning each dive cycle to a season based on the date of its occurrence. This statistic was also used to test for night–day differences in time spent near the surface for each individual deployment.

Finally, we tested for moon effects on nighttime dive metrics using a generalized additive model (GAM) of behaviors as Gaussian distributions predicted by the multiplicative effects of lunar phase and elevation (cyclic and non-cyclic penalized cubic regression splines, respectively) in the *R* package 'mgcv' (Wood, 2017).

Results

Deployment Summary

The final dataset used in the analysis contained 245.4 d of data from 10 individuals from May 2011 to August 2015, with an average deployment duration of 24.5 d (min. 6.1, max. 83.2; Table 2). Three whales were tagged in winter, four in spring, and three in summer (BpTag073 is referred to as a summer deployment, despite having begun in late May, since it continued into early August).

In our field effort, 13 tags were deployed on 13 unique individuals. Reactions to tagging were categorized as follows: "No reaction" (n = 2), "Low-level" (n = 10), and "Moderate" (n = 1). These reactions were generally transient; the strongest noted behavioral reaction was a single tail flick. One tag transmitted for 46.2 d, but irregularities in the depth data suggested the pressure transducer malfunctioned early in the deployment and, thus, the deployment was removed from the dataset. Two other tags had poor location and dive data throughput (transmission durations = 5.7 and 13.2 d); they were also excluded from analyses. Two clearly aberrant dives were identified in a single BL message from BpTag058 (2013-04-05 17:44:22, with depth of 1,679 m; 2013-04-05 14:57:42, with depth of 801 m). The message appeared to have been corrupted; thus, all five dive cycles transmitted via that Argos message were removed from the analysis. Of the 10 tagged animals with sufficient location data, all but two stayed within the SCB for the transmission duration of the tag (Figure 2). The exceptions were BpTag072 (transmission duration = 33 d), which traveled to waters north of the San Francisco Bay area (Figure S1), and BpTag063 (transmission duration = 83 d), which traveled south into Mexican waters off Baja California before returning to the SCB (Figure S2). Most tagged animals

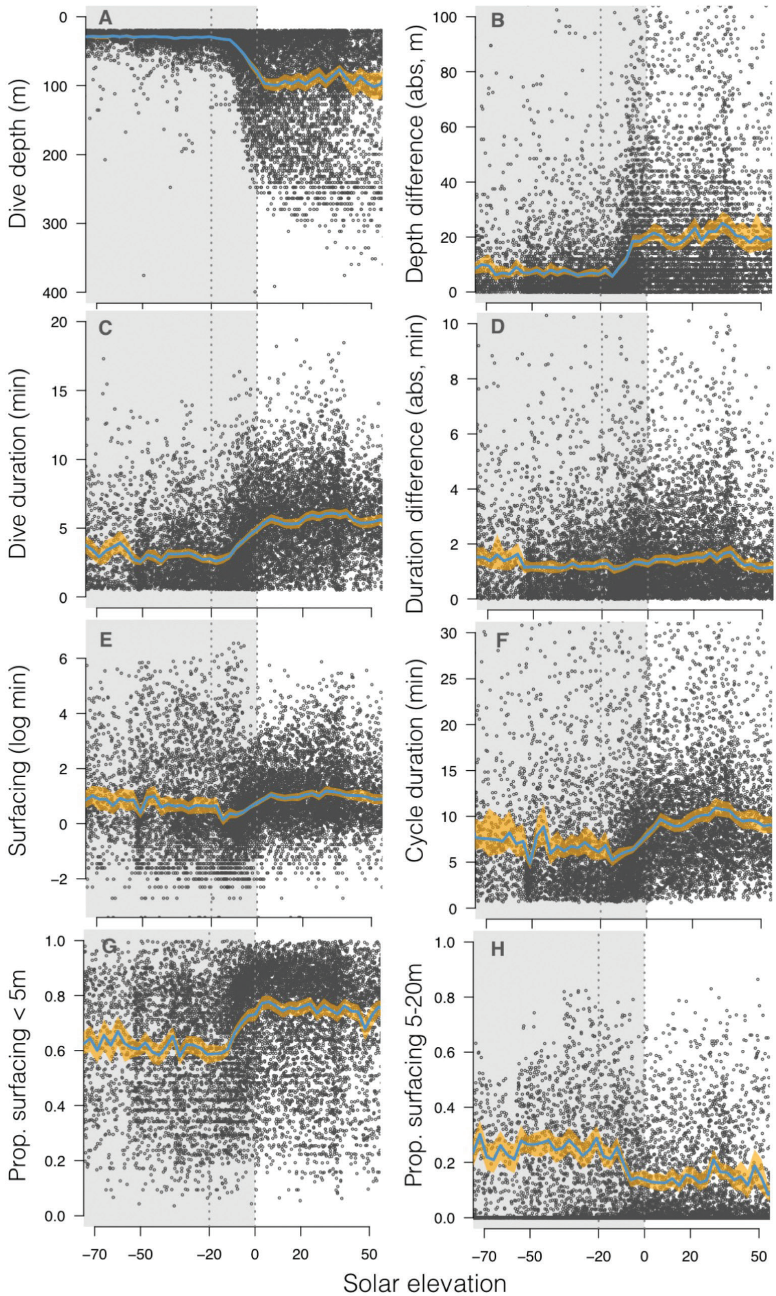

Figure 1. Changes in dive parameters as functions of solar elevation, revealing diel modes in fin whale (*Balaenoptera physalus*) dive behavior. Each black dot is the parameter value for a dive cycle. The blue line is a running median (window size = 3° of solar elevation), and the orange area is the 95% confidence interval of the median calculated using Wilcoxon sign rank test. Vertical dashed lines delineate the transition zone between the nighttime dive mode (< -20° of solar elevation) and daytime dive mode (> 0° of solar elevation). (A) Dive depth (m), (B) absolute value of depth difference between paired dives, (C) dive duration (min), (D) absolute value of dive duration difference (min), (E) duration of surfacing occurring between the paired dives (log-scale min), (F) proportion of paired dive sequence duration spent shallower than 30 m depth, (G) proportion of surfacing spent shallower than 5 m, and (H) proportion of surfacing spent between 5 and 20 m.

spent the majority of their time within a designated U.S. Navy training range, and there was considerable overlap with regions of elevated shipping activity associated with ports (Figures 2B & 2C; Table S1). (The supplemental table and figures are available on the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147.)

Diel Dive Behaviors

Two dominant diel modes of diving behavior were strongly evident in the data: (1) shallow nighttime diving and (2) variable daytime diving that included very deep (max. 527 m) dives (Figure 3). These modes were separated by crepuscular periods during which sequential dives generally increased in depth around dawn and decreased in depth around dusk (Figure 4).

Table 2. Summary of tag deployments

					Dives					Surface intervals		
	Deployment	Sample size			Depth (m)		Duration (min)			Duration (min)		
ID	Date	Days	Dives	Surf.	Median	Max.	Median	Min.	Max.	Median	Min.	Max.
BpTag048	5 Jan 2013	28.2	2,142	2,140	32.0	527.5	3.70	0.50	18.20	2.00	0.03	350.0
BpTag050	5 Jan 2013	6.1	510	510	29.0	247.5	2.00	0.50	14.47	1.50	0.03	313.0
BpTag058	23 March 2013	14.2	1,235	1,236	38.0	375.5	3.00	0.50	13.80	1.60	0.07	652.0
BpTag059	29 March 2013	10.3	382	382	39.0	263.5	4.70	0.50	14.90	2.80	0.07	235.5
BpTag060	29 March 2013	11.2	620	622	38.0	311.5	3.00	0.57	13.07	1.50	0.03	355.0
BpTag061	29 March 2013	11.1	350	350	65.5	271.5	4.50	0.53	10.00	2.30	0.13	572.0
BpTag063	19 May 2013	83.2	1,539	1,536	69.5	391.5	4.80	0.53	12.40	3.10	0.03	511.0
BpTag066	10 Jan 2014	21.3	1,198	1,197	38.0	303.5	6.20	0.53	21.80	2.40	0.03	695.0
BpTag072*	30 June 2015	32.9	2,245	2,242	87.5	367.5	5.70	0.50	15.70	2.00	0.10	411.0
BpTag073*	24 Aug 2015	26.9	1,207	1,211	51.5	271.5	4.70	0.57	16.20	1.50	0.10	633.0
	Mean	24.5	1,143	1,143	48.8	333.1	4.23	0.52	15.05	2.07	0.06	472.75
	SD	22.5	689	689	19.2	85.2	1.30	0.03	3.26	0.57	0.04	160.93
	Min.	6.1	350	350	29.0	247.5	2.00	0.50	10.00	1.50	0.03	235.50
	Max.	83.2	2,245	2,242	87.5	527.5	6.20	0.57	21.80	3.10	0.13	695.00
	Total	245.4	11,428	11,426								

*Tags with surface cutoff of 2 m. All other tags used a cutoff of 5 m.

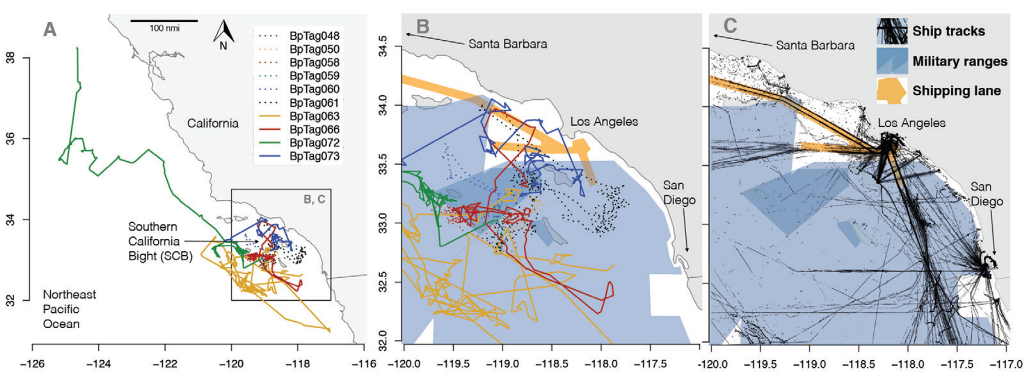

Figure 2. (A) Tracks of the 10 fin whale tags used in this analysis in northeast Pacific waters off southern California; (B) close-up of tag tracks and select human activities in the Southern California Bight (SCB); the military range complexes depicted here (layered blue polygons) include the Pt. Mugu Sea Range and the Southern California Range Complex; (C) ship tracks (black dots) from commercial shipping in July 2014, sourced using the Automatic Information Service (AIS; www.marinecadastre.gov); military vessel activity is not transmitted via AIS and, therefore, is not available for display here. Note that shipping activity is not confined to the Santa Barbara–Los Angeles shipping lane (orange polygon).

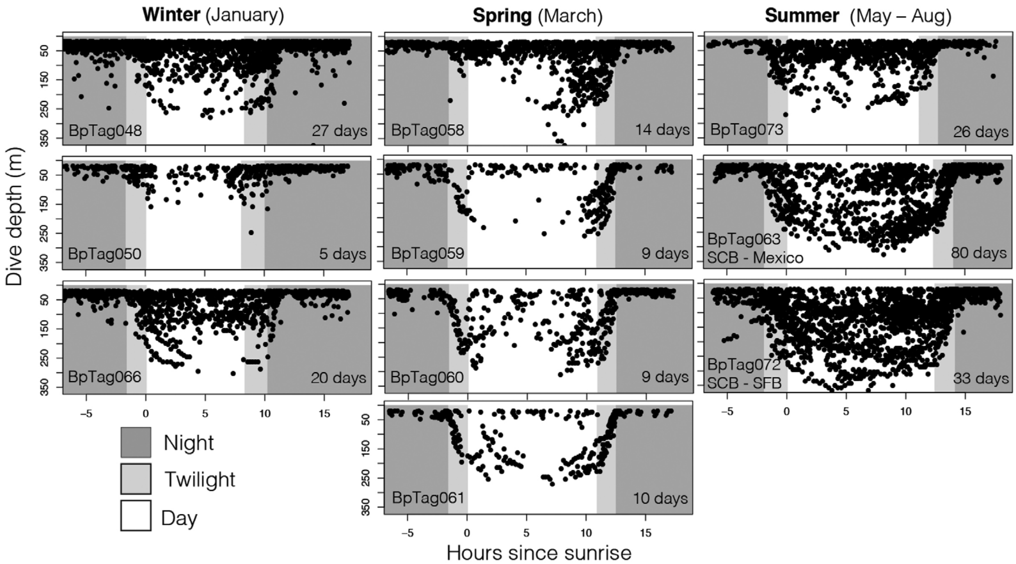

Figure 3. Diel patterns in dive depth for each tagged animal organized according to season of deployment. Time is presented as hours since sunrise; shaded areas represent nighttime. Sunset is placed at the mean time of sunset in each deployment. All deployments occurred in the SCB unless noted otherwise. SFB = San Francisco Bay. Note that deployment BpTag063, which is listed under "Summer," began on 19 May and lasted 80 d.

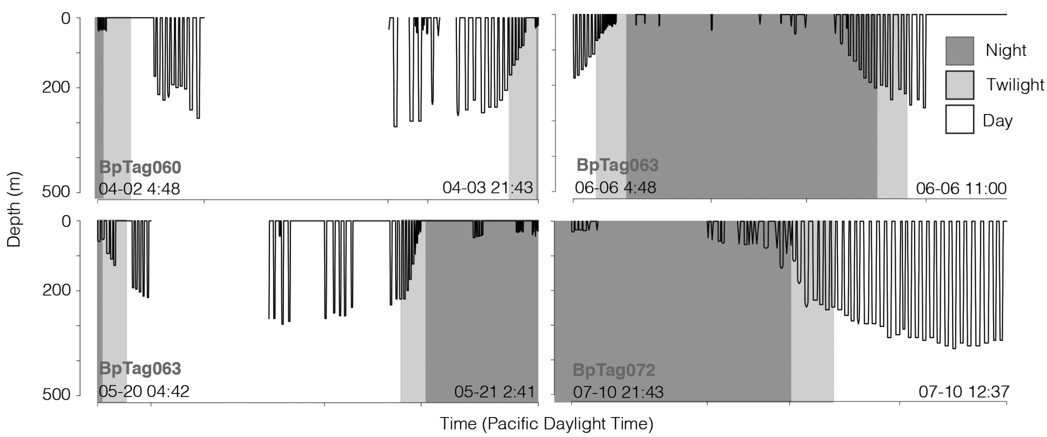

Figure 4. Examples of dive traces with apparent crepuscular foraging behavior; segments with no trace are gaps in the behavior log.

For most dive metrics, significant differences were found between night- and daytime records (Table 3; Figure 5). With data from all seasons combined (Figures 1 & 5), nighttime dives were shallower (pseudomedian: 29.5 m) and shorter (pseudomedian: 3.02 min) than dives during the day (pseudomedians: 95.5 m and 5.68 min). When surfacings and dives were combined into dive cycles, the percentage of time spent shallower than 20 m was greater at night (pseudomedian: 57%) than during the day (pseudomedian: 42%). This diel difference in vertical habitat use increased across depth windows: the pseudomedian percentage of time spent shallower than 30 m was 81% at night and 49% during the day (Figures 1 & 6). The percentage of time spent shallower than 40 m was nearly 100% at night and 55% during the day when whales were routinely diving beyond this depth between surfacings.

While fin whales spent more time in the upper 20 m of the water column at night, the percentage

Table 3. Sample sizes of dive cycle datasets used in tests for diel dive behavior (Figure 5)

	Winter	Spring	Summer	Total
Day	1,504	1,729	2,734	5,967
Night	1,469	824	493	2,786
Total	2,973	2,553	3,227	8,753

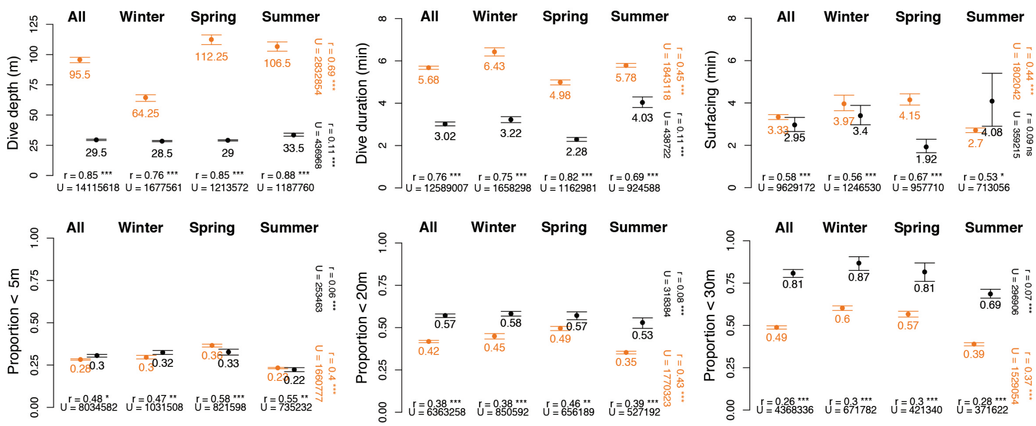

Figure 5. Metrics of dive behaviors and surface activity split by diel period (day = orange; night = black) and by season. Pseudomedian (dots and numbers) and 95% CIs of the median (bars) are calculated with a Mann-Whitney U test. Statistics along pane bottoms are U test comparisons of day and night data; statistics along the right margin of panes are U test comparisons of winter and summer metrics during day and night. Significance key: ns = not significant; * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

of that time spent at the surface itself (shallower than 5 m) was lower at night (~65%) than during the day (~75%), and the proportion spent between 5 and 20 m was correspondingly higher at night than during the day (Figure 1). When viewed as a percentage of the entire dive cycle, whales ultimately spent slightly more time at the surface at night (30%) than during the day (28%), though the difference was statistically negligible.

Based on GAM results, lunar phase and altitude were statistically significant predictors in the case of most nighttime behavior metrics, but they explained only a small portion (1 to 7%) of deviance, and visual inspection of spline smoothing plots did not reveal stark trends (Figure S3). Based on these plots, lunar phase exhibited a greater (though still minor) effect than lunar elevation upon fin whale surface use. Fin whales spent more time within 20 m of the surface when the moon was least illuminated and was below the horizon.

Seasonal Variation in Diel Dive Behaviors

Diel patterns in diving metrics also varied by season (Table 3; Figure 5). Daytime dives in summer (pseudomedian: 106.5 m) were nearly twice as deep as those in winter (pseudomedian: 64.25 m; $p < 0.001$). Nighttime dives (pseudomedian: 33.5 m) were slightly deeper in summer than in winter (pseudomedian: 28.5 m; $p < 0.001$). The percentage of dive cycles spent at the surface (< 5 m) was greater in winter nights (pseudomedian: 32%) than in summer nights (pseudomedian: 22%; $p < 0.001$). The percentage of the dive cycles spent shallower than 20 m was greatest during nights in winter (pseudomedian: 58%) and least during summer days (pseudomedian: 35%) (Figures 5 & 6).

Although spring dive behaviors were not statistically compared to the other seasons due to small sample size, pseudomedians indicate that the percentage of time spent above 20 m depth was comparatively high both day (49%) and night (57%), the depth difference between day and night dives was high (days: 112.25 m; nights: 29.00 m), and the percentage of dive cycles spent at the surface (< 5 m) was also high during the spring (days: 36%; nights: 33%).

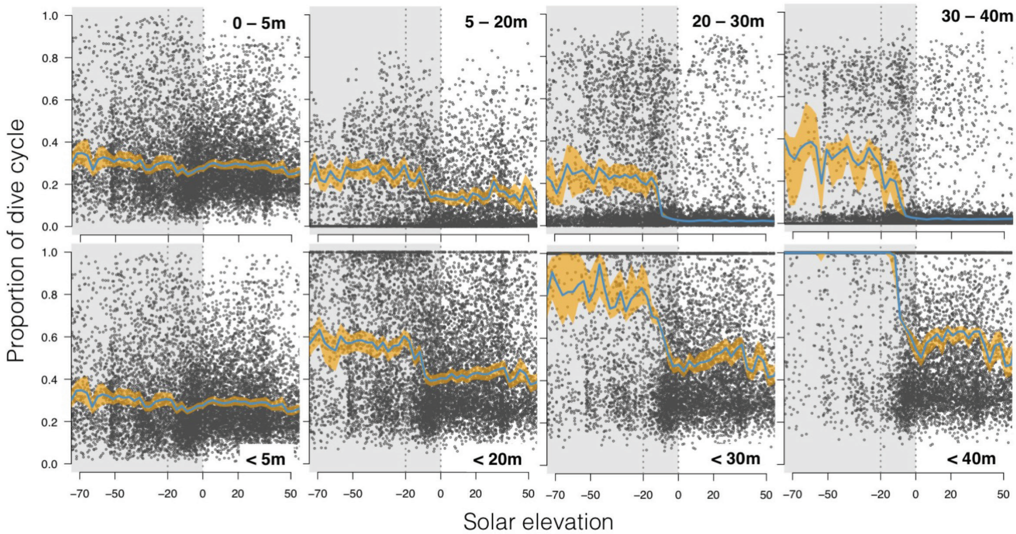

Figure 6. Changes in surface activity as functions of solar elevation for all deployments. The top row is time spent *within* intervals of increasing depth; the bottom row is time spent *shallower than* increasing depths. Each black dot is the proportion value for a dive cycle. The blue line is a running median (window size = 3° of solar elevation); the orange area is the 95%CI of the median calculated using Wilcoxon sign rank test; and the vertical dashed lines delineate the transition zone between the nighttime dive mode (less than -20° of solar elevation) and daytime dive mode (greater than 0° of solar elevation).

Individual and Geographic Variability

The above diel patterns were generally consistent across tagged individuals (Figures S4 & S5). Nighttime use of waters above 30 m was statistically greater than daytime for each tag deployment when tested individually ($p < 0.001$ for all tags). Increased nighttime use of waters above 20 m was significant for seven out of 10 tags (not significant: BpTag060, BpTag063, and BpTag066; five tags were significant at $p < 0.001$, one tag at $p < 0.01$, and one tag at $p < 0.05$).

The dominant seasonal and diel behavioral patterns of the two animals that left the SCB during their tag deployment (Figures S1 & S2) were also consistent with those described for the entire dataset regardless of the fin whale's location. The percentage of nighttime dive cycles spent shallower than 20 m increased when BpTag072 moved north into central Californian waters (Figure S1) but did not change during the day. There was no apparent difference in time spent at the surface (< 5 m) between the regions this whale visited. Inter-regional nighttime data were sparse for BpTag063, but daytime data suggest that time spent at the surface was greater in the SCB than in waters off Mexico (Figure S2).

Discussion

Dive data from 10 tagged fin whales in the SCB confirmed the prevalence of diel modes in the diving behavior of this species, with dives becoming progressively deeper at dawn and shallower at dusk. These patterns are similar to those observed in other baleen whales and are believed to be associated with the vertical migration of prey throughout the day as well as likely changes in foraging efficiency associated with light availability for these visual predators (Panigada et al., 1999; Calambokidis et al., 2007; Friedlaender et al., 2009, 2013, 2015, 2016; Burrows et al., 2016; Tyson et al., 2016). Daytime dives varied most in depth and duration from dive to dive, and also between seasons, potentially in response to shifts in prey availability, including prey type, behavior, and depth within the water column, as well as seasonal changes in the whales' nutritional needs and social behavior as fin whales are thought to breed seasonally like most baleen whales (Aguilar, 2009). However, fin whales also engage in daytime surface lunge feeding when prey conditions allow (Kot, 2005). While data limitations of these tags preclude the identification of surface feeding, if it were occurring during these deployments, it would contribute to the variability in daytime dive metrics and also negatively bias any differences seen between day- and nighttime surface behavior.

These whales spent roughly a third of their time at or immediately below the surface regardless of time of day—likely a reflection of their basic respiratory needs. However, use of the upper water column increased substantially at night when they remained almost exclusively within 40 m of the surface and spent nearly 60% of their time shallower than 20 m. Lunar phase is known to alter vertical migration behavior in euphausiids (Benoit-Bird et al., 2009), causing them to migrate closer to the surface more often on dark nights than on well-lit ones. It is also possible that lunar illumination would delineate schools enough to enable nighttime feeding. Such effects could explain why the proportion of nighttime spent within 20 m of the surface increased slightly during new moons (Figure S3). Our finding that lunar phase had more of an effect than lunar elevation is consistent with the findings in Benoit-Bird et al. (2009), which they interpreted as evidence that micronekton and zooplankton migrate vertically according to an "endogenous lunar rhythm" (p. 1789) rather than in response to changing light levels.

The trend toward increased use of the upper water column at night was evident in all three seasons tested but most pronounced in winter when 58% of nighttime behavior was spent shallower than 20 m, and 87% was spent above 30 m. Summertime dive data collected here extended the published records for both dive depth (Panigada et al., 1999; Figure S6) and duration for fin whales. Fin whales, like other aquatic mammals, are thought to swim well below the surface to minimize wave drag and thrust loss (Fish, 1993). Hui (1989) postulated that swimming efficiency increases when a cetacean is deeper than one-half of one body length. Based on a mean adult length of 21.6 m (Aguilar, 2009), the theoretical efficiency boundary for northeast Pacific fin whales is 10.8 m. It is reasonable to expect fin whales to swim at or near this boundary when they are not pursuing prey at depth (Owen et al., 2016), and this may explain why the fin whales we tagged used 5 to 20 m depths more intensively at night when deep foraging was infrequent and presumably less effective (Figure 6).

The patterns we observed in vertical habitat use correspondingly contribute to diel and seasonal patterns of exposure to surface-associated risks such as vessel collisions and military exercises. McKenna et al. (2015) modeled ship-strike risk using a ship draft of 8 m and a zone of hydrodynamic risk beneath the ship's hull equal to two times the draft (Silber et al., 2010)—in their case, 16 m. The actual vertical danger zone posed by ships in an area depends on the distribution of their drafts, which are, in turn, functions of vessel type and size, cargo loads, fuel levels, speeds, and other factors. Even with this variability in ship drafts, anytime whales are above 20 m depth, they are likely within the strike danger zone of many large ships as defined by McKenna et al. (2015). This risk is particularly high at night when whales spend a disproportionate amount of time between 5 and 20 m depth and cannot be detected visually even when at the actual surface. This effect is strongest in winter and is compounded by the increase in length of the winter night itself.

The year-round habitat suitability of the SCB for fin whales (Scales et al., 2017) likely explains their abundance relative to other large cetaceans in the region (Campbell et al., 2015). This year-round presence and their heavy use of the upper water column, particularly at times when they cannot be avoided, may explain why the fin whale is the most often ship-struck of the region's large whales (NOAA unpub. data, 2009-2015), despite the lower probability of detecting struck animals relative to other species given their predominantly offshore distribution (Rockwood et al., 2017). Data from two animals that left the SCB suggest that these patterns are likely not limited to southern California and should be considered anywhere fin whales co-occur with elevated levels of vessel traffic (Figures S1 & S2). With evidence of site fidelity by at least some individual whales (Falcone & Schorr, 2014; Scales et al., 2017), this increased risk to ship strike may also increase the risk of population-level impacts for whales in this region.

The SCB is a bustling marine area replete with anthropogenic disturbances such as noise, debris, and pollution, along with high volumes of ship traffic. Prolonged near-surface activity increases exposure to all of these potential risks (Hildebrand, 2009; Cassoff et al., 2011). These diel patterns in vertical habitat use provide some predictable patterns of risk for fin whales within the SCB, and likely beyond it. Additional data, including fin whale responses to vessels, and temporal and geographic patterns of anthropogenic activity, are required to fully understand the scope of these risks; however, any proposal to mitigate surface-associated risks to fin whales should be robust to the nighttime patterns elucidated herein.

Acknowledgments

We thank the U.S. Navy, including N45, the Living Marine Resources program, and the U.S. Navy Pacific Fleet, for funding both fieldwork and tags. We thank our collaborators from the Naval Undersea Warfare Center, in particular David J. Moretti, and the Marine Mammal Monitoring on Naval Ranges group, as well as the Cascadia Research Collective. The staff of the Southern California Offshore Range and personnel on

San Clemente Island provided essential logistical support. We also wish to acknowledge the support of the Office of Naval Research and Brad Hanson of the NOAA Northwest Fisheries Science Center for tag development.

Literature Cited

Aguilar, A. (2009). Fin whale: *Balaenoptera physalus*. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 368-371). San Diego, CA: Academic Press/Elsevier. https://doi.org/10.1016/B978-0-12-373553-9.00102-4

Andrews, R. D., Pitman, R. L., & Ballance, L. T. (2008). Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica. *Polar Biology*, *31*(12), 1461-1468. https://doi.org/10.1007/s00300-008-0487-z

Aoki, K., Amano, M., Yoshioka, M., Mori, K., Tokuda, D., & Miyazaki, N. (2007). Diel diving behavior of sperm whales off Japan. *Marine Ecology Progress Series*, *349*, 277-287. https://doi.org/10.3354/meps07068

Baird, R. W., Borsani, J. F., Hanson, M. B., & Tyack, P. L. (2002). Diving and night-time behaviour of long-finned pilot whales in the Ligurian Sea. *Marine Ecology Progress Series*, *237*, 301-305. https://doi.org/10.3354/meps237301

Baird, R. W., Ligon, A. D., Hooker, S. K., & Gorgone, A. M. (2001). Subsurface and nighttime behaviour of Pantropical spotted dolphins in Hawai'i. *Canadian Journal of Zoology*, *79*(6), 988-996. https://doi.org/10.1139/z01-070

Benoit-Bird, K. J., Au, W. W. L., & Wisdoma, D. W. (2009). Nocturnal light and lunar cycle effects on diel migration of micronekton. *Limnology & Oceanography*, *54*(5), 1789-1800. https://doi.org/10.4319/lo.2009.54.5.1789

Berrow, S. D., McHugh, B., Glynn, D., McGovern, E., Parsons, K. M., Baird, R. W., & Hooker, S. K. (2002). Organochlorine concentrations in resident bottlenose dolphins (*Tursiops truncatus*) in the Shannon estuary, Ireland. *Marine Pollution Bulletin*, *44*, 1296-1303.

Bivand, R., & Lewin-Koh, N. (2017). maptools*: Tools for reading and handling spatial objects*. R *package version 0.9-2*. Retrieved from https://CRAN.R-project.org/package=maptools

Burrows, J. A., Johnston, D. W., Straley, J. M., Chenoweth, E. M., Ware, C., Curtice, C., . . . Friedlaender, A. S. (2016). Prey density and depth affect the fine-scale foraging behavior of humpback whales *Megaptera novaeangliae* in Sitka Sound, Alaska, USA. *Marine Ecology Progress Series*, *561*, 245-260. https://doi.org/10.3354/meps11906

Calambokidis, J., Schorr, G. S., Steiger, G. H., Francis, J., Bakhtari, M., Marshall, G., . . . Robertson, D. (2007). Insights into the underwater diving, feeding, and calling behavior of blue whales from a suction-cup-attached video-imaging tag (CRITTERCAM). *Marine Technological Society Journal*, *41*(4), 19-29. https://doi.org/10.4031/002533207787441980

Campbell, G. S., Thomas, L., Whitaker, K., Douglas, A., Calambokidis, J., & Hildebrand, J. A. (2015). Inter-annual and seasonal trends in cetacean distribution, density and abundance in waters off southern California. *Deep Sea Research II*, *112*, 143-157. https://doi.org/10.1016/j.dsr2.2014.10.008

Cassoff, R. M., Moore, K. M., McLellan, W. A., Barco, S. G., Rotstein, D. S., & Moore, M. J. (2011). Lethal entanglement in baleen whales. *Diseases of Aquatic Organisms*, *96*, 175-185.

Douglas, D. C., Weinzierl, R., Davidson, C. S., Kays, R., Wikelski, M., & Bohrer, G. (2012). Moderating Argos location errors in animal tracking data. *Methods in Ecology & Evolution*, *3*(6), 999-1007. https://doi.org/10.1111/j.2041-210X.2012.00245.x

Falcone, E. A., & Schorr, G. S. (2014). *Distribution and demographics of marine mammals in SOCAL through photo-identification, genetics, and satellite telemetry* (Chief of Naval Operations, Energy and Environmental Readiness Division No. NPS-OC-14-005CR). Monterey, CA: Naval Postgraduate School. https://doi.org/10.21236/ADA613907

Fish, F. E. (1993). Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. *Australian Journal of Zoology*, *42*(1), 79-101. https://doi.org/10.1071/ZO9940079

Friedlaender, A. S., Goldbogen, J. A., Hazen, E. L., Calambokidis, J., & Southall, B. L. (2015). Feeding performance by sympatric blue and fin whales exploiting a common prey resource. *Marine Mammal Science*, *31*(1), 345-354. https://doi.org/10.1111/mms.12134

Friedlaender, A. S., Tyson, R. B., Stimpert, A. K., Read, A. J., & Nowacek, D. P. (2013). Extreme diel variation in the feeding behavior of humpback whales along the western Antarctic Peninsula during autumn. *Marine Ecology Progress Series*, *494*, 281-289. https://doi.org/10.3354/meps10541

Friedlaender, A. S., Hazen, E. L., Nowacek, D. P., Halpin, P. N., Ware, C., Weinrich, M. T., . . . Wiley, D. (2009). Diel changes in humpback whale *Megaptera novaeangliae* feeding behavior in response to sand lance *Ammodytes* spp. behavior and distribution. *Marine Ecology Progress Series*, *395*, 91-100. https://doi.org/10.3354/meps08003

Friedlaender, A. S., Johnston, D. W., Tyson, R. B., Kaltenberg, A., Goldbogen, J. A., Stimpert, A. K., . . . Nowacek, D. P. (2016). Multiple-stage decisions in a marine central-place forager. *Royal Society Open Science*, *3*, 160043. https://doi.org/10.1098/rsos.160043

Hildebrand, J. A. (2009). Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series*, *395*, 5-20. https://doi.org/10.3354/meps08353

Hollander, M., & Wolfe, D. A. (1973). *Nonparametric statistical methods*. New York: John Wiley & Sons.

Hui, C. A. (1989). Surfacing behavior and ventilation in free-ranging dolphins. *Journal of Mammalogy*, *70*(4), 833-835. https://doi.org/10.2307/1381722

Jeanniard-du-Dot, T., Holland, K., Schorr, G. S., & Vo, D. (2017). Motes enhance data recovery from satellite-relayed biologgers and can facilitate collaborative research into marine habitat utilization. *Animal Biotelemetry*, *5*(1), 17. https://doi.org/10.1186/s40317-017-0132-0

Kot, B. W. (2005). *Rorqual whale surface-feeding strategies: Biomechanical aspects of feeding anatomy and exploitation of prey aggregations along tidal fronts* (Master's thesis). University of California, Los Angeles.

McKenna, M. F., Calambokidis, J., Oleson, E. M., Laist, D. W., & Goldbogen, J. A. (2015). Simultaneous tracking of blue whales and large ships demonstrates limited behavioral responses for avoiding collisions. *Endangered Species Research*, *27*(3), 219-232. https://doi.org/10.3354/esr00666

McKenna, M. F., Soldevilla, M., Oleson, E., Wiggins, S., & Hildebrand, J. A. (2009). Increased underwater noise levels in the Santa Barbara Channel from commercial ship traffic and the potential impact on blue whales (*Balaenoptera physalus*). In C. C. Damiani & D. K. Garcelon (Eds.), *Proceedings of the 7th California Islands Symposium Institute for Wildlife Studies* (pp. 141-149), Arcata, CA.

Owen, K., Jenner, C. S., Jenner, M-N. M., & Andrews, R. D. (2016). A week in the life of a pygmy blue whale: Migratory dive depth overlaps with large vessel drafts. *Animal Biotelemetry*, *4*, 17. https://doi.org/10.1186/s40317-016-0109-4

Panigada, S., Pesante, G., Zanardelli, M., & Oehen, S. (2003). Day and night-time behaviour of fin whales in the western Ligurian Sea. *Proceedings of the Conference on Oceans*, San Diego, CA.

Panigada, S., Zanardelli, M., Canese, S., & Jahoda, M. (1999). How deep can baleen whales dive? *Marine Ecology Progress Series*, *187*, 309-311. https://doi.org/10.3354/meps187309

R Core Team. (2018). R*: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org

Rockwood, R. C., Calambokidis, J., & Jahncke, J. (2017). High mortality of blue, humpback and fin whales from modeling of vessel collisions on the U.S. West Coast suggests population impacts and insufficient protection. *PLOS ONE*, *12*(8), e0183052. https://doi.org/10.1371/journal.pone.0183052

Scales, K. L., Schorr, G. S., Hazen, E. L., Bogard, S. J., Miller, P. I., Andrews, R. D., . . . Falcone, E. A. (2017). Should I stay or should I go? Modelling year-round habitat suitability and drivers of residency for fin whales in the California Current. *Diversity & Distribution*, *23*, 1204-1215. https://doi.org/10.1111/ddi.12611

Schorr, G. S., Falcone, E. A., Moretti, D. J., & Andrews, R. D. (2014). First long-term behavioral records from Cuvier's beaked whales (*Ziphius cavirostris*) reveal record-breaking dives. *PLOS ONE*, *9*(3), e92633. https://doi.org/10.1371/journal.pone.0092633

Silber, G. K., Slutsky, J., & Bettridge, S. (2010). Hydrodynamics of a ship/whale collision. *Journal of Experimental Marine Biology & Ecology*, *391*(1-2), 10-19. https://doi.org/10.1016/j.jembe.2010.05.013

Širović, A., Williams, L. N., Kerosky, S. M., Wiggins, S. M., & Hildebrand, J. A. (2013). Temporal separation of two fin whale call types across the eastern North Pacific. *Marine Biology*, *160*(1), 47-57. https://doi.org/10.1007/s00227-012-2061-z

Tyson, R. B., Friedlaender, A. S., & Nowacek, D. P. (2016). Does optimal foraging theory predict the foraging performance of a large air-breathing marine predator? *Animal Behaviour*, *116*, 223-235. https://doi.org/10.1016/j.anbehav.2016.03.034

Wildlife Computers. (2017). *Wildlife Computers* Splash10 *tag and host user guide*. Retrieved from https://wildlifecomputers.com/wp-content/uploads/manuals/MK10-User-Guide.pdf

Wood, S. N. (2017). *Generalized additive models: An introduction with* R (2nd ed.). New York: Chapman and Hall/CRC. https://doi.org/10.1201/9781315370279